II.—*On the use of the term Homology in modern Zoology, and the distinction between Homogenetic and Homoplastic agreements.* By E. RAY LANKESTER, B.A. Oxon.

WHILST the adoption of the theory of evolution has broken down the notions at one time held by zoologists and botanists as to the existence of more or less symmetrical classes and groups in the organic world, established by some inherent law of Nature which limited her productive powers to arbitrary special plans or types of structure, and has taught us to see, in the variously isolated and variously connected kinds of animals and plants, simply the parts of one great genealogical tree, which have become detached and separated from one another in a thousand different degrees, through the operation of the great destroyer Time, yet certain terms and ideas are still in use which belonged to the old Platonic school, and have not been defined afresh in accordance with the doctrine of descent. The notion of the possibility of classifying organisms accurately by means of division into large groups of equal value and significance, these again being divided into smaller groups of equal subordinate value, and so on, is still almost universally prevalent, although one of the first conclusions to which we are led by a consideration of Darwin's doctrine is that the groups into which we may be able to cast the few and scattered samples of organic development known to us must be in every way most unequal and dissimilar, the line which we can draw in one case being sharp and clear, in another much less certain and definite, sometimes including a vast variety of minor groups, sometimes embracing definitely marked large groups, in no case offering us examples of two series of forms strictly alike in extent and significance; and thus it is rendered impossible to indicate the genetic relations of organisms by the use of the neat and symmetrical system of terms generally employed (consisting of kingdom, subkingdom, class, order, family, &c.). To do this adequately, additional terms are required (and, indeed, have been proposed), and the important fact has to be held in mind that we have not to search out a supposed symmetrical disposition of organisms existing in nature, but to simply indicate as clearly as we can the sequence of forms and the innumerably various gaps in the series.

The term "homology" belongs to the Platonic school, but is nevertheless used without hesitation by those who reject the views of that school. Professor Owen (who first clearly defined this term, in developing those researches into the agreements of essential structure under various modifications by which the biologists of the first part of this century so much advanced science) would understand by *homologue* "the same organ in different animals under every variety of form and function;" by *analogue*, "a part or organ in one animal which has the same function as another part or organ in a different animal." But how can the sameness (if we may use the word) of an organ under every variety of form and function be established or investigated? This is, and always has been, the stumbling-block in the study of homologies without the light of evolutionism; for, to settle this question of sameness, an ideal "type" of a group of organisms under study had to be evolved from the human mind, after study of the component members of the group; and then it could be asserted that organs might be said to be the "same" in two animals which had a common representative in the ideal type.

This reference to an ideal type was the only criterion o homology; and yet we find those who have adopted the doctrine of evolution making use of the term "homology" without any explanation. The study of homologies was brought under a very important influence from the appreciation of the value of developmental changes in indicating the similarities or distinctions of organs; and before the appearance of Mr. Darwin's theory many zoologists were turning to embryology as a surer guide than ideal archetypes in tracing the identities of structure in organisms; so that, refusing to commit themselves to the Platonic theory, they were ready to receive the flood of light and explanation which the doctrine of descent shed upon the meaning and nature of homologies.

What, then, are we to suppose that an evolutionist means when he asserts that an organ A in one animal is homologous with an organ B in another animal? It is clear that he cannot consistently have the same meaning as a Platonist; and yet it appears that, from the force of habit or some accidental cause, the term homology *is* used at the present time in the old sense by many authors who accept the doctrine of evolution, or at any rate not with any definite meaning which has been agreed upon by those who belong to the new school.

Without particularizing the authors whose views are alluded to, we may mention the attempt to trace the *homologies* of the bones of the skull in detail through the vertebrate series, the *homology* of the chain of nerve-ganglia of Arthropoda with the sympathetic of Vertebrata, the *homology* of the four cavities of the heart and also of the individual muscles of the limbs in Sauropsida and Mammalia, and especially the so-called *serial homologies* of the fore and hind limbs in Vertebrata and of the teeth of the upper and lower jaws.

Without doubt the majority of evolutionists would agree that by asserting an organ A in an animal α to be homologous with an organ B in an animal β, they mean that in some common ancestor κ the organs A and B were represented by an organ C, and that α and β have inherited their organs A and B from κ. Though this is the definition of homology which we should expect from an evolutionist, it is yet not that which seems to be implied in the cases above cited; and on investigation it appears that there is something more contained in the Platonist's term "homologue," which must be separated and distinguished from the idea of genetic community of origin. It will be found, in fact, necessary to have two terms in place of the one "homologue," and to broadly distinguish the nature of the resemblances to which they are applied. Structures which are genetically related, in so far as they have a single representative in a common ancestor, may be called *homogenous*. We may trace an *homogeny* between them, and speak of one as the *homogen* of the other. Thus the fore limbs of Mammalia, Sauropsida, Batrachia, and Fishes may be called, so far as their most general structure is concerned, *homogenous*, but only so far as relates to general structure; for if we endeavour to trace these groups back to a common ancestor, we find that, by the time that ancestor is reached, the limb has become a very simple form, and that which Mammalia, Sauropsida, Batrachia, and Fishes have inherited from this common ancestor is but the rude outlines of an appendage: it is only thus far that their limbs can be called homogenous. If, however, we compare the fore limb of Sauropsida and Mammalia, it is possible to go a step further with the homogeny; for the common ancestor of these groups we may suppose to be (for the sake of illustration) among the immediate ancestors of the Batrachia; and so far as the fore limbs of Mammalia and Sauropsida present evidence of that simple skeleton and system of muscles which we have reason to believe their præ-Batrachian ancestor possessed, we may assert their homogeny, but no further: details not traceable to and inherited from the ancestor cannot be homogenous. And now, if we turn to the examples of structures whose homologies have been recently discussed by writers who, there is good reason to believe, accept the doctrine of evolution, we shall see that in tracing *homologies* they are not confining themselves to the elucidation of what it is here proposed to term *homogenies*. Since, in all probability, the Vertebrata have diverged from the stock which gave rise to the Arthropoda at a point in the series where the nervous syste mis of the simplest and most rudimentary kind, it is only to a small extent that there is homogeny between the chain of nerve-ganglia of Arthropods and the sympathetic ganglion-system of Vertebrata—merely an agreement which is so general that we can only say that the nervous system as such in the two cases is in the most general way homogenous, and must seek for some other cause to account for the more detailed resemblance of the insect's nerve-chain to the vertebrate sympathetic. In this case we see that in discussing so-called "homology," two kinds of relation have been in question. Again, it may perhaps be admitted that the common ancestor of the osseous Fishes and Mammalia had a skull of decidedly undifferentiated character, with a much less amount of segmentation than is observed in the skulls of either of these groups. It is only in so far as they have parts represented in the common ancestor that we can trace *homogeny* in these groups; and yet the *homology* of a vast number of bones in the skulls of the two is discussed and pointed out. In particular may be mentioned the mammalian incus, malleus, and other parts in their region which have been identified homologically with *particular* bones in the suspensorium of the lower jaw of the fish. It will be allowed that the *homogeny* is of a much less detailed kind, and will only admit of the assertion of a genetic relation between the *regions* in which these bones arise, the particular result of segmentation in each case being *not* homogenous, since the common ancestor of osseous fish and mammalia was in all probability a fish in which segmentation of the lower jaw and suspensorium had been carried to a very small extent. So, too, with regard to the homologies of the same bones with the Sauropsidan suspensorium*. The homogenetical agreement can be one of no greater detail than is indicated by the condition of this region in the supposed common ancestor of Mammalia and Sauropsida; and it does not appear probable that the incus and malleus, or the quadrate and articulare, were represented by similarly segmented bones in their common ancestor. To take another case, the four cavities of the bird's heart are generally regarded as homologous with the four cavities of the mamma-

* The supposed cases of homology here given are used to illustrate the principle under discussion. The latest views which have been advanced by Prof. Huxley on the homologies of the malleus and incus and neighbouring parts are acceptable if we recognize homogeny, since he dwells rather on the identity of the cartilaginous arches than on the correspondence of individual segments; but I am not sure that he means to speak of homogenetic relation when he says, "The operculum and suboperculum (of fishes) together answer undoubtedly to potential hard parts in the mammalian concha of the ear" (Brit. Med. Journ. (Abstract) 1869, p. 375).

lian heart; but since the common ancestor of mammals and birds in all probability had but three cavities to its heart, the ventricles are only *homogenetic* as a whole, and not each to each. The disposition of the aorta and the important light thrown on the origin of the muscular right auriculo-ventricular valve of the bird's heart by comparison with an Ophidian or Lacertian heart, harmonize decidedly with the conclusion that the right ventricle of the bird is not homogenetic with the right ventricle of the mammal. But it is said to be homologous. Why? What is there more involved in the term homology which here, again, as also with regard to the bones of the skull, is not implied in the term homogeny? When it is sought to establish a detailed homology between the muscles of the pectoro-humeral region in Mammalia, Birds, and Reptiles (as, for instance, is done by my friend and teacher, Professor Rolleston, who concludes that the mammalian subclavius is the homologue of the pectoralis secundus of the bird, and of the epicoraco-humeral of the Iguana, and the mammalian coraco-brachialis longus of the pectoralis tertius of the bird and of the middle part of the coraco-brachialis of reptiles), we surely are not to understand that these muscles are homogenetic, that the common ancestor of Mammalia and Sauropsida possessed all these muscles, and has transmitted them to its descendants. The common stock of these groups most certainly had not such a specialization of this part of its muscular structures. What, then, is it that produces so close a resemblance in the disposition of these parts as to lead one to speak of homology? What is the other quantity covered by the term homology over and above homogeny?

The consideration of one more case, that of serial homologies, will bring us to this: Unless it be maintained that the vertebrate animal is an aggregate of two individuals, one represented by the head and arms, the other by the legs, no genetic identity can be established between the fore and hind limbs. And since no one will maintain such a constitution for the Vertebrata (though it is exceedingly probable that the earliest segmentation which they exhibit is a remnant of such a history), the possibility of serial homogeny is out of the question in Vertebrata, though the segments of Arthropoda, Vermes, and other tertiary aggregates present it. And yet we speak of serial homologies; and it is possible to trace a very remarkable correspondence between the bones and muscles of the fore and hind limbs. What is the nature of the correspondence between fore and hind limb which is called "serial homology?" If we can ascertain this, we may expect to ascertain at the same time the nature of the correspondence which is not homogenetic and yet is recorded as "homology" in the study of the cranial bones, of the bones and muscles of the extremities, and of other organs. The answer to this inquiry appears to be found in the following considerations. When identical or nearly similar forces, or environments, act on two or more parts of an organism which are exactly or nearly alike, the resulting modifications of the various parts will be exactly or nearly alike. Further, if, instead of similar parts in the same organism, we suppose the same forces to act on parts in two organisms, which parts are exactly or nearly alike and sometimes homogenetic, the resulting correspondences called forth in the several parts in the two organisms will be nearly or exactly alike. There will be, I imagine, no kind of difficulty to the evolutionist or student of Mr. Herbert Spencer's writings in admitting the above propositions; and it is in accordance with the principle they set forth that serial homologies and much else which, together with what is here distinguished as homogeny, has been included under homology may be explained. I propose to call this kind of agreement *homóplasis* or *homóplasy*. The fore legs have a homoplastic agreement with the hind legs, the four extremities being, in their simpler form (e. g. *Proteus*, which must have had ancestors with quite rudimentary hind legs), very closely similar in structure and function. To a very considerable extent the movement and support required from the fore and hind limbs in subsequent developments of this stock, whether towards Mammalia or Sauropsida, would be the same; and hence the muscular and skeletal parts would agree in many striking details, these details serving as the groundwork for further modifications when the character of a flying, grasping, or offensive organ was assumed by either pair of extremities*. The muscles of the pectoro-humeral region are homogenetic in a general way in mammals and Sauropsida; but such details of agreement as that between the pectoralis major of mammals and the gracilis of *Iguana*, the subclavius and the deeper head of the pectineus, the coraco-brachialis and part of the obturator externus, we must set down to the fact that they are to a great degree homoplasts,—similar forces or require-

* The concomitant variation of fore and hind limb in such matters as feather-growth seems to point to a somewhat closer relation between these parts; but it is quite conceivable that such a nutritional relation should arise in the course of time by a sort of delicate balancing of the forces of the organism, which would cause the disturbance of equilibrium in one part to affect simultaneously another part equally and similarly. Organs which stand in this nutritional relation to one another may be termed homotrophic; such are teeth and hair, eyes and ears, and others enumerated by Mr. Darwin, as well as fore and hind limbs.

ments operating on similar materials in the two stocks, the Mammalian and Sauropsidan, having produced results in the way of structure which have a certain agreement. What, exactly, is to be ascribed to homogeny, and what to homoplasy, in the relations of this series of structures, is a matter for careful consideration. As was remarked above, the right ventricle of the bird's heart is not homogenous with the right ventricle of the mammal's heart, nor the left with the left; but the two cavities in each case are homoplastic—the same conditions as regards the maintenance of animal heat and other matters belonging to the circulation, which evoked or were the cause of the perpetuation of this structure in the one case having equally operated in the other. As to the bones of the skull, the room for diversity is not very great when the homogenous basis is given which all higher Vertebrata have inherited from a common ancestor; but there can be no doubt that many of the bones in the fish's skull are not homogenous with those of other Vertebrata, whilst they appear to be related as homoplasts. That similar forms may arise in this way in the skulls of two divergent stocks, and lead to close correspondences which are not traceable to homogeny, is indicated by the fact that membrane-bones corresponding in position and relations in the skulls of one group to cartilage-bones in the skulls of another group are observed*. The membrane-bone in this case is certainly not homogenous with the cartilage-bone; but it is homoplastic with it; and in the same way it is very probable that membrane-bones in two skulls are in some cases only homoplasts, though they may have been the subject of speculation as to their homology. The mammalian malleus and mandible present an homogeny of the general region only, when compared with the bones of the suspensorium and lower jaw of the fish, the individual bones of which, as well as the opercular bones, are not represented in the mammalian skull by corresponding individual bones, and not even by homoplastic developments. The Sauropsidan suspensorium, in being segmented, presents a closer homoplastic agreement with that of osseous fish; and probably a true homogenetic correspondence is to be admitted in the quadrato-articular articulation of Fishes and Sauropsida.

It may be said that the term "analogy," already in use, is sufficient to indicate what is here termed "homoplasy;" but analogy has had a wider signification given to it, in which it is

* As an example, the cartilage-bone in the fish's skull, which Mr. Parker proposes to call pterotic, till lately considered the homologue of the squamous in mammals, may be cited.

found very useful to employ it, and it could not be used with any accuracy in place of homoplasy. *Any* two organs having the same function are analogous, whether closely resembling each other in their structure and relation to other parts or not; and it is well to retain the word in that wide sense. Homoplasy includes all cases of close resemblance of form which are not traceable to homogeny, all *details* of agreement not homogenous, in structures which are broadly homogenous, as well as in structures having no genetic affinity.

There may be other less direct causes at work in producing homoplasy besides an agreement in environment or external evoking conditions; such a cause is indicated in the remarkable cases grouped by Mr. Darwin as correlations of growth, and for which the term *homotrophy* may perhaps be found useful.

An illustration of the distinction between homoplastic and homogenetic agreement in form may be seen in the possible origin of the forms of the weapons and utensils of various races of men. Two races, A and B, without communication, *may* devise a stone axe or a canoe of similar form: the resemblance is in this case homoplastic. The inventors have learnt in the same school, indeed; but that school is the school of necessity, as Professor Huxley once observed with regard to the Indian stone implements. In the course of time the axe or canoe is improved on and perfected in various ways by the race A, and this particular form of instrument becomes widely spread and slightly modified in various branches of the race. The various modifications are all homogenous, traceable as they are to one original pattern which has been improved upon. They have, however, still merely a homoplastic agreement with the instruments of the race B, which may have become similarly improved.

Besides the cases of simple homoplasy which have not been discriminated from homogeny, but indicated under the common term homology, there are others which may be cited, which have less commonly or never been accounted for by calling them cases of homology. Among the simplest of these, we have the jointing of an appendage, such as the antenna of an insect and of a crustacean, the individual joints of which are homoplastic, though they have never been considered homologous—or, again, the calcareous shell of a cirripede and a multivalve mollusk, which are to a great degree homoplasts, though their homology has not been maintained for many years. The beak of a bird is to a considerable extent homoplastic with the beak of a chelonian, the dorsal and caudal fins of a cetacean with those of some fish, the setæ of *Acan-*

thobdellea with those of Chætopods; but zoologists would hesitate to assert homology in these cases, and it certainly seems improbable that there is homogeny. What Mr. Spencer calls "superinduced segmentation," hitherto included by many zoologists as serial homology, falls under simple homoplasy, the detailed resemblances of the vertebræ being thus explained, though it is possible that there is an obscured homogenous segmentation indicated in the earliest stages of vertebrate development.

I trust now to have said sufficient to illustrate the distinction which I wish to draw between homogeny and homoplasy, and to have shown a probability that a good deal of the latter has been associated with the former under one head, "homology." It is less likely to cause confusion if we have a new term than if we amend an old one, which is my reason for not retaining "homology." It is not improbable that homoplasy may admit of further analysis; but it is sufficient here to distinguish it from homogeny. I do not propose to defend against criticism the cases I have used in illustration. The views suggested with regard to particular cases are open to much discussion, and the views alluded to as being commonly held may in some instances be not very widely prevalent. This, however, does not affect the matter in hand. Concrete cases are given merely with a view to illustration, and to render clear what is the relative significance of the terms "homology," "homogeny," and "homoplasy."

What is put forward here is this,—that under the term "homology," belonging to another philosophy, evolutionists have described and do describe two kinds of agreement—the one, now proposed to be called "homogeny," depending simply on the inheritance of a common part, the other, proposed to be called "homoplasy," depending on a common action of evoking causes or moulding environment on such homogenous parts, or on parts which for other reasons offer a likeness of material to begin with. In distinguishing these two factors of a common result we are only recognizing the principle of a plurality of causes tending to a common end, which is elsewhere recognizable and has been pointed out in biological phenomena. The explanation of the phenomena by the one law of homology is a part of that tendency to view Nature as more simple and more easily mastered than she really is, against which Bacon cautions us.

I am persuaded that some valuable results may be obtained from an investigation of the numerous problems of homology by the light which the discrimination of homogenous and homoplastic formations can afford. The discrimination is a matter of time and labour, but is feasible. Besides the homologies of the vertebrate skeleton and muscles, I would mention the various vascular systems of the Invertebrata as likely to be better understood in this manner. The vascular system of leeches, with its hæmoglobin, is not homogenous with that of Chætopods, though closely homoplastic with it: its relation to the nervous system, segment-organs, its development, and the probable ancestral relations of the Leeches and Trematodes lead to this conclusion. Yet most zoologists would consider these two vascular systems homologous, or perhaps only qualify the term by refusing to regard them as *strictly* homologous.

Again, the hæmochyle or blood-lymph system of Vertebrates has no homogen, or but a very rudimentary one, in the other groups of animals. The vascular fluid of mollusks and insects has a homoplastic agreement with one part of the vertebrate hæmochyle, viz. the lymph, whilst the hæmoglobin of annelids and of the plasma of some insects' and mollusks' vascular fluid corresponds functionally with the red corpuscles.

Another distinction, of more importance, which a consideration of homogeny and homoplasy suggests, relates to the segmentation in various groups of the Annulosa. Leaving the question as to the origin of this segmentation, by arrested gemmation or otherwise, on one side, we are led to conclude that in any case such repetition is not necessarily a proof of affinity, is not necessarily homogenous in the animals compared, but may be simply homoplastic. The Annelida, on the one side, and the Arthropoda, on the other, are probably entirely unrelated, so far as their segmentation is concerned, each having sprung from a distinct unisegmental ancestor, the primitive Annelidan and Arthropodan having been possibly very little alike, even in their unisegmental stage, and having only a more remote ancestral connexion, difficult to conjecture. Thus, then, the ganglion-chain of the two groups, and their points of contact in tegumentary development, sense-organs, &c., are simply homoplastic, and not homogenous.

Zoology has been for some time embarrassed with the reference of all segmented Invertebrata to a common type, and the supposed homology of their segmented structures. This difficulty may, it is suggested, be possibly solved by the admission of true zooid-segmentation as being frequently due to homoplasy, and not by any means necessarily an indication of genetic affinity.